MARINE TURBELLARIA (ACOELA) FROM NORTH QUEENSLAND

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Seven species of free-living acoels are now known from Australia. A new genus, new species and new combination of haploposthiid acoels are reported. They are *Waminoa litus* gen. et sp. nov., two non-sexual *Waminoa* sp., *Convolutriloba hastifera* sp. nov., and *C. japonica* (Katô, 1951) comb. nov.. The diagnosis for the genus *Convolutriloba* Hendelberg and Åkesson, 1988, is emended. The heterogeneous convolutid genus *Amphiscolops* is reviewed, and the genus *Heterochaerus* reinstated and emended to accommodate *H. australis* Haswell, 1905, and *H. sargassi* (Hyman, 1939) comb. nov. New records of *H. australis* and *Convolutriloba* cf. *retrogemma* are reported. A key to free-living acoel genera described from Australian waters is provided. □ *Acoela, tropical marine flatworms, taxonomy, key, Waminoa, Convolutriloba, Amphiscolops, Heterochaerus.*

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Little is known of the free-living turbellarian acoel fauna of Australia. Until now only two species, both intertidal convolutids, have been described. They are *Amphiscolops australis* from Port Jackson, New South Wales, (Haswell, 1905) and *Wulguru cuspidata* from Townsville, north Queensland (Winsor, 1988).

This paper is mainly based upon collections of acoels from north Queensland waters. It includes descriptions of new taxa, a reappraisal of the genera *Convolutriloba* (Haploposthiidae), *Amphiscolops* and *Heterochaerus* (Convolutidae), and a key to genera of free-living Acoela described from Australia.

MATERIALS AND METHODS

Squash preparations of specimens were examined by differential interference contrast microscopy. Other material was narcotized with 7.5% magnesium chloride and fixed in marine Bouin's fluid. Specimens were processed to paraffin wax, serially sectioned at 5-7µm and stained with iron haematoxylin-eosin, trichrome stains and selected histochemical methods (Winsor, 1984). Wholemounts were stained by carmine, iron haematoxylin and histochemical methods.

Specimens for electron microscopy were fixed in 2.5% glutaraldehyde in sea-water. For scanning electron microscopy (SEM) specimens were critical point dried, gold coated and examined in secondary mode using an ETEC-SEM. Tissues for transmission electron microscopy (TEM) were post fixed in 1% osmium tetroxide, processed to Spurr's resin, sectioned at 70-90nm, stained with uranyl acetate and lead citrate, and examined using a JOEL FX200 TEM.

Terminology follows that proposed by Cannon (1986). Type and voucher specimens prefixed G are lodged with the Queensland Museum (Townsville Branch). Material from the Australian Museum, Sydney is prefixed AM.W.

The following abbreviations are used in the Figures: a - anterior end, bursa; as - algal symbiont; b - bursa; bc - bursal canal; bg - basiphil glands; c - cuboidal epithelium; cc - concrement cell; cm - cell mass (? sensory function); d - duct; e - eye; em - epidermal musculature; f - lateral body fold; fa - female antrum; fo - frontal organ; fv - false seminal vesicle; g - ganglion; m - mouth; mc - matrix cells ; n - nucleus; o - oocyte; ov - ovary; ps - prostatic secretions; pt - pit, frontal organ; r - rhabdoids; s - sperm; sb - sagittocystoblast; sg - sagittocyst; st - statocyst-statolith; sv - seminal vesicle; t - testes; y - yolk-producing part, ovary; ♂ - male genital pore; ♀ - female genital pore

Haploposthiidae Westblad, 1948
Waminoa gen. nov.

DIAGNOSIS

Haploposthiidae discoid to obcordate in shape; colour results from pigments and symbiotic algae; often with two coexisting species of algal symbionts; brain insunk; mouth ventral and in

posterior third of body; rhabdoids present; ovaries and testes paired; with sub-terminal male genital pore; male atrium ciliated; seminal bursa with paired lateral bursal canals. Statocyst-statolith, eyes, frontal gland, female genital pore and penis absent. Epizoic on corals.

TYPE OF GENUS

Waminoa litus sp. nov.

ETYMOLOGY

The genus name *Waminoa* is an Aboriginal word meaning companion and alludes to the occurrence of this acoel on corals. The specific epithet is from the Greek *litos* meaning plain or unadorned, refers to the drab appearance of the species.

Waminoa litus sp. nov.
(Fig. 1a-f)

Haplodiscus sp. (in part) Trench and Winsor, 1987

MATERIAL EXAMINED

TYPE LOCALITY: Geoffrey Bay, Magnetic Island, 19°08'S, 146°50' E. Collected by G. Bull from soft coral, 9.9.1979.

HOLOTYPE: G23003, four microslides, longitudinal sagittal 5μm sections, iron haematoxylin and eosin.

PARATYPE: G23004, wholemount, iron haematoxylin.

OTHER SPECIMENS EXAMINED: Geoffrey Bay, Magnetic Island, collected by P. Osmond from the soft coral *Sarcophyton* sp. March, 1983; 30.4.1985; 21.5.86; 9.12.87; 13.4.89; Nelly Bay, Magnetic Island. Collected by P. Osmond from *Sarcophyton* sp. 13.4.1989.

DESCRIPTION

At rest living specimens are obcordate in shape and cinnamon- brown in colour with a translucent margin. Pigmentation is due to algal symbionts. The body is slightly narrower anteriorly than posteriorly, with a pronounced mid-caudal notch. Sexual specimens attain about 2mm maximum width. The mid-dorsal region is generally slightly elevated and less pigmented than the rest of the body.

Dorsal cilia are 5μm long and are less numerous than the ventral cilia, 7μm long. The dorsal epidermis is 2.5μm thick and the ventral epidermis 5μm thick. Longer sensory cilia are sparsely distributed over the body. Underlying the epidermis are circular, oblique and longitudinal muscle layers. The dorso-ventral musculature is weakly developed. Circular muscles surround the mouth and male genital pore.

The brain is insunk and consists of a bilobed ganglion. Immediately posterior to the ganglion is a non-glandular cellular mass 25μm by 50μm, possibly sensory in function. The cells are slightly ellipsoid, 6-8μm diameter with large evenly staining nuclei, prominent nucleoli and pale evenly staining cytoplasm.

A statocyst-statolith, eyes, frontal gland complex and concrement cells are absent.

Two species of algal symbionts are present. An *Amphidinium* sp. measuring 16μm-24μm diameter and a smaller *Symbiodinium* sp. approximately 8μm in diameter. The algae lie immediately below the epidermal musculature, and in some specimens appear almost completely to occupy the central parenchyma.

Fusiform packets, measuring 27μm x 5μm, of translucent acicular rhabdoids are present in the dorsal epithelium. There are two types of non-rhabditiform glands: a granular type fairly evenly distributed over the dorsal surface, slightly more abundant anteriorly and absent in the region of the caudal notch. The granular secretions are found to be composed of neutral mucopolysaccharides. The other type of gland is mainly concentrated along the margins and ventral surface: These glands have amorphous acid mucopolysaccharide secretions.

In living specimens numerous spherical refractile bodies were observed underlying the epidermis. In stained sections they are acidophilic and measure 5-7μm diameter. They do not appear to be associated with any gland or particular structure, but lie within the parenchyma. These bodies give negative histochemical reactions for mucins and lipids.

The mouth lies ventrally in the posterior third of the body. The endocytium contains amorphous sedimentary particulate matter, diatoms and remains of unidentified crustacea.

Testes are paired and lie dorso-laterally to the ovaries. Sperm pass posteriorly and accumulate before passing to the male antrum. The male genital pore is situated ventrally and subterminally on a muscular papilla. The ciliated male antrum, which appears to be a simple invagination of the ventral epidermis, communicates with a duct. The duct is well defined distally but indistinct proximally. There is no definite penial structure.

The ovaries are paired, ventrally situated and extend posteriorly behind the mouth. The seminal bursa lies ventro-medially and posterior to

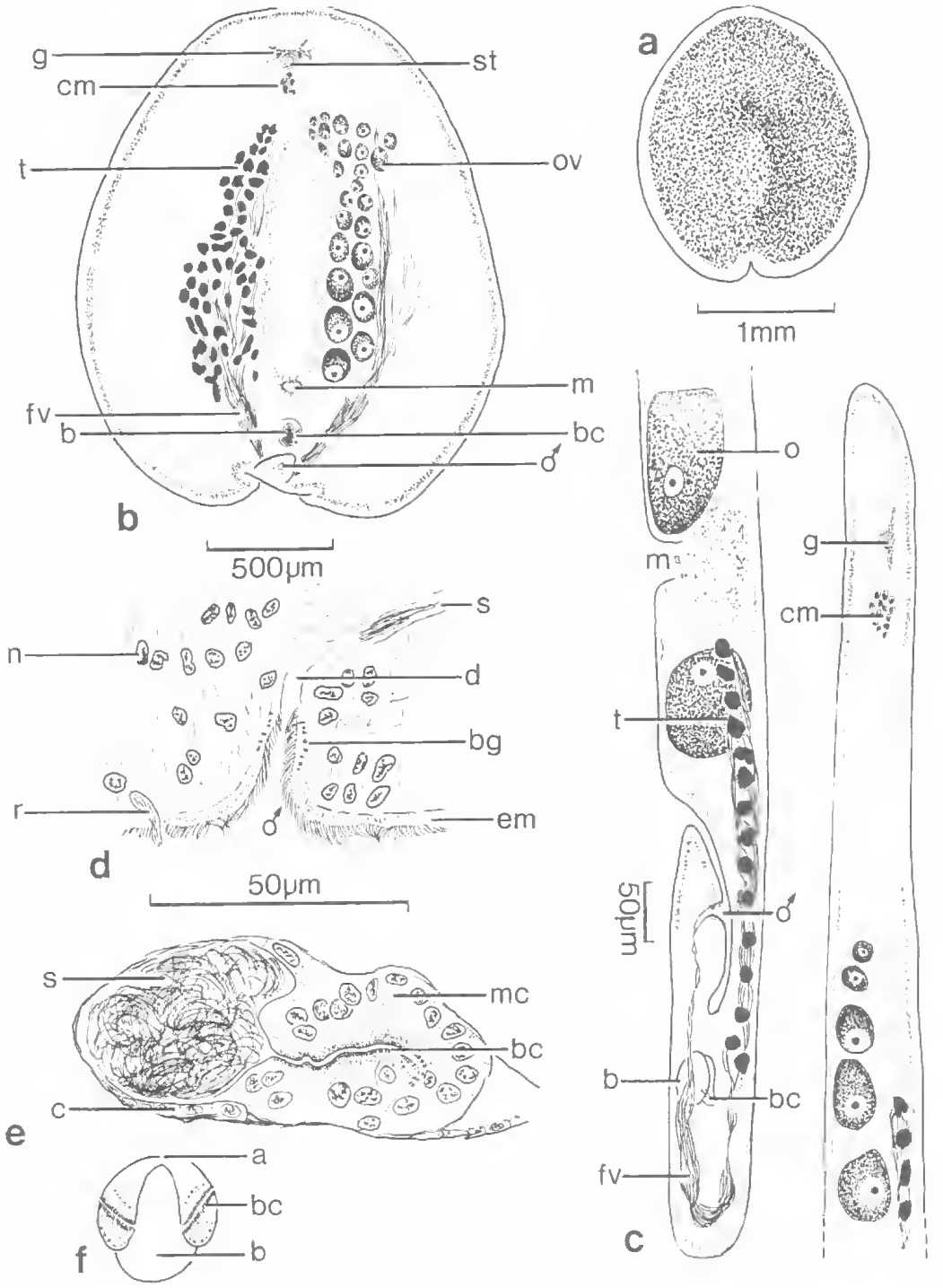

FIG. 1. *Wamtnoa litus*. (a) Dorsal aspect, living specimen, (b) ventral aspect, whole mount (for clarity the ovary on right side is not shown), (c) longitudinal section (d) male copulatory apparatus, (e) bursa and bursal canal, and (f) dorsal view of bursa showing bursal canals (unscaled sketch).

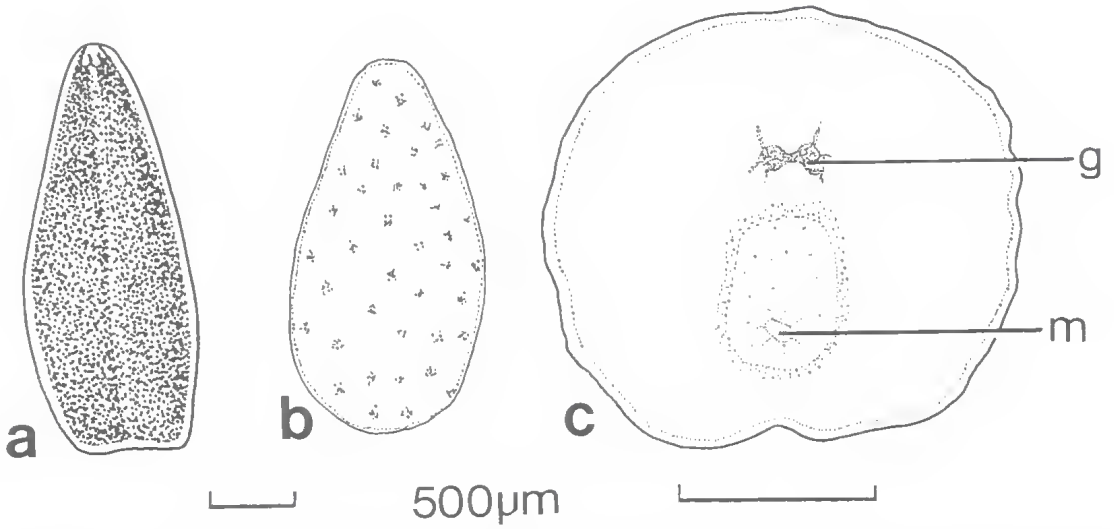

FIG. 2. *Waminoa* sp. 1. (a) dorsal aspect, living specimen by transmitted light, and (b) by incident light (black dendritic clusters represent pattern of concrement cells),(c) ventral aspect, wholemount.

the base of the muscular papilla and is partially surrounded antero-ventrally by a cellular mass, in part comprised of matrix cells. From either side of this structure two short weakly sclerotised bursal canals project antero-laterally into the parenchyma. A female genital pore is absent. No duct communicates with the bursa.

Waminoa sp. 1
(Fig. 2a-c)

MATERIAL EXAMINED

LOCALITY: Marine aquarium Australian Institute of Marine Science, Townsville. Collected by Dr S. Collard from corals, 19.11. 1981, and fixed in mercuric chloride-acetic acid.

VOUCHER SPECIMENS: G23011 Grenacher's carmine stained wholemount and G23012 a single microslide, horizontal 6µm trichrome stained sections.

DESCRIPTION

Living specimens are approximately 2mm long and ovate to obcordate in shape. Examined under incident light, the dorso-lateral surfaces are mottled with dendritic iridescent-white concrement which is retained in fixed specimens. In colour and pattern the acoels exactly resemble the retracted polyps on the coral on which they were found. Under transmitted light these acoels appear translucent brown, less dense along the dorsal mid-line. The colour is due to symbiotic algae. Three unpigmented zones are present anteriorly.

Fixed specimens are approximately 1.2mm diameter. The mouth is ventral and situated in the posterior third of the body. Statocyst-statolith, eyes and frontal gland are absent. The bilobed cerebral ganglion is insunk. There are two species of algal symbionts: the smaller species 6-7µm diameter and the larger less numerous species 9-12.5µm diameter. Male and female gonads and copulatory organs are absent.

Waminoa sp. 2

MATERIAL EXAMINED

LOCALITY: Pandora Reef, 18°49'S, 146°26'E. Collected by P. Alino from *Acropora longicyathus* 22.11.1987, and fixed in the field in marine Bouin's solution.

VOUCHER SPECIMENS: G23013 Grenacher's carmine stained wholemount and G23014 a single microslide of serial horizontal 6µm trichrome stained sections.

DESCRIPTION

Specimens are 1mm diameter, discoid with slight mid-caudal notch with mouth in the ventral posterior third of the body. The colour when live was not noted. There are no dendritic flecks on the dorso-lateral surface. Two species of algal symbionts are present: a numerous small species 7-8.5µm diameter, and a larger less numerous species 11-14µm diameter. Statocyst, eyes, frontal gland, male and female gonads and copulatory organs absent.

SYSTEMATIC DISCUSSION

In external morphology *Waminoa* species closely resemble those of the planktonic convolutid *Haplodiscus* Weldon, 1888. However with ventral subterminal male gonopore, simple tubular male antrum, and penis absent or possibly present only as a small papilla, *Waminoa* is assigned to the Haploposthiidae as defined by Cannon (1986).

Within the Haploposthiidae *Waminoa* is clearly differentiated from the other eleven genera by a combination of characters: the presence of two coexisting species of algal symbionts from which *Waminoa* species derive their colour, presence of rhabdoids, paired ovary and testis, an isolated seminal bursa with two weakly sclerotised bursal canals, and absence of statocyst, eyes, and frontal gland. *Waminoa* is closest to *Pseudohaplogonaria* Dörjes, 1968, from which it is distinguished chiefly by the presence of a well formed seminal bursa with paired lateral bursal canals, and from *Deuterogonaria* Dörjes, 1968, by the presence of the paired bursal canals and absence of a vesicular granulorum.

The presence of an *Amphidinium* sp. and *Symbiodinium* sp. in the tissues of *Waminoa*, described by Trench and Winsor (1987) represents the first observation of two dinoflagellate species co-existing in the same cell of the invertebrate host, though Yamasu and Okazaki (1987) have reported the presence of two different algal symbionts in two species of the convolutid *Amphiscolops*.

At present *Waminoa litus* is the only species found with copulatory organs. Although there is no obvious penial structure in this species, the atrium may evert to form a penis. In two mature specimens a small ventral sub-terminal papilla is present in the region corresponding to the position of the male pore. Unfortunately the absence of sperm in the immediate vicinity of the papilla makes it difficult to confirm the nature of this structure.

Waminoa sp.1 is distinguished from the other two species by the presence of concrement. *Waminoa* sp. 2 found on a scleractinian coral, is smaller in diameter than *W. litus* and *Waminoa* sp.1. As host specificity of the species is unknown it is considered prudent at present to distinguish *W. litus* and *Waminoa* sp. 2 though they may prove to be conspecific.

The *Haplodiscus sp.* of Yamasu and Okazaki (1987) from Sesoko Island (Ryukyu Islands, Japan) found on coral is possibly a species of *Waminoa*. In their preliminary report the authors remark that 'no specimens bore male and female germ cells or genital organs. Body is brown due to symbiotic algae, an *Amphidinium* type dinoflagellate.'

Convolutriloba Hendelberg and Åkesson (1988)(emend)

DIAGNOSIS

Haploposthiidae with colour and pattern resulting from pigment and symbiotic algae; frontal gland present; statocyst may be absent; brain insunk; mouth ventral; rhabdoids and sagittocysts present; ovaries and testes paired; ovaries divided into oocyte-producing and yolk-producing parts; with two ventral genital openings; male antrum ciliated passing directly into seminal vesicle; without penis; female antrum and vagina ciliated; seminal bursa with single sclerotised bursal canal.

TYPE OF GENUS

Convolutriloba retrogemma Hendelberg and Åkesson, 1988

Convolutriloba cf. **retrogemma** Hendelberg and Åkesson, 1988.

MATERIAL EXAMINED

LOCALITY: The marine aquarium, University of New South Wales, found on juvenile *Tridacna gigas* clams. Specimens fixed in Bouin's fluid were forwarded by L. Goggin.

VOUCHER SPECIMENS: G23007 wholemount stained Grenacher's carmine, and G23008 four microslides of serial horizontal 6μm sections, haematoxylin and eosin.

DESCRIPTION

Non-sexual specimens 1-2mm long are similar in external morphology to *C. retrogemma* and correspond to the original description. Sagittocysts are not present in whole mounts or sectioned specimens. Algal symbionts measured 5.4- 9μm diameter.

Convolutriloba hastifera sp. nov. (Figs 3a-f, 4a-f)

MATERIAL EXAMINED

TYPE LOCALITY: Australian Institute of Marine Science (AIMS) Cape Cleveland, near Townsville,

north Queensland. Collected from the aquarium by Dr Clive Wilkinson 21.9.1983.

HOLOTYPE: G23005 four microslides, longitudinal saggital sections 5μm, trichrome stain.

PARATYPE: G23006 wholemount, Gower's carmine.

OTHER SPECIMENS EXAMINED. Sexual specimens found on soft coral, Geoffrey Bay, Magnetic Island, collected by G. Bull 9.9.1979; specimens collected from the marine aquarium at AIMS by Dr Clive Wilkinson; November 1983, 27.11.84, 30.1.85.

ETYMOLOGY

The specific epithet *hastifera* is derived from the Latin *hasta* - a spear, and *ferens* - bearing, and refers to prominent anterior batteries of sagittocysts present in the species.

DESCRIPTION

Living specimens at rest measure up to 3mm long and 1.5mm wide. The body is dorsoventrally flattened, broad and rounded anteriorly. It narrows slightly in the mid third of the body, then broadens posteriorly with two lateral caudal lobes and smaller median lobe. In life the median lobe is generally slightly elevated and does not project posteriorly beyond the lateral lobes.

The ground colour is a translucent greenish-yellow to greenish-brown and is primarily the result of symbiotic algae which are fairly uniformly distributed dorsally and ventrally. A fine orange-red pigment is concentrated dorsally mainly around the base of the median caudal lobe and along the lateral body margins. It is scattered sparsely mid dorsally and anteriorly but is absent ventrally.

Iridescent-white dendritic flecks seen under incident lighting are present over the whole dorso-lateral surface apart from two unpigmented, slightly depressed areas (eye fields) about 36μm in diameter situated anteriorly. Aggregations of flecks mid-anteriorly, mid-posteriorly and laterally at the 'waist' form the points of a cruciform pattern.

Both dorsal and ventral epidermis are 2μm in thickness. The entire body surface is covered by cilia 5-6μm long. Sensory cilia 14-15μm long are spaced 75-85μm apart. Underlying the epidermis are the usual circular, oblique and longitudinal muscle layers. Dorso-ventral muscles are abundant, particularly laterally.

Two eyes are present within the unpigmented anterior areas. Each eye is oval, measures 19μm antero-posteriorly and 34μm medio-laterally, and is composed of minute reddish brown granules. The cerebral ganglion is insunk and bilobed. There is no statocyst-statolith.

Algal symbionts (Prasinophyceae, ? *Platymonas*) measure 7-12μm diameter and underlie the cutaneous body musculature dorsally and ventrally.

Three types of rhabdoids are present. The most conspicuous are sagittocysts, refractile acicular bodies 18-20μm long and about 2.5-3.6μm diameter with central stylet 1μm diameter, lying in the parenchyma at right angles to the surface with only the tips protruding from the epithelium. They are particularly numerous in batteries anteriorly, and to a lesser extent dorso-ventrally and laterally. They are sparse posteriorly. Ventrally they surround the male pore.

Histochemically the sagittocysts are strongly basiphilic and periodic acid-Schiff positive. Sagittocystoblasts are located deeper within the body and ultrastructurally comprise a lateral nucleus and thin granular cytoplasm surrounding the sagittocyst. The sagittocyst consists of a fibrillar, concentrically lamellate cortex about 3.5-4μm diameter surrounding a central stylet. The stylet is a 1μm diameter membrane bound tube. The wall is approximately 300nm thick and composed of short fibrils, with an inner thin electron dense band. In the central lumen is an eccentrically situated electron dense rod about 140nm diameter.

The conspicuous reddish-orange epidermal pigment noted macroscopically is due to orange-coloured fusiform and bacilliform rhabdoids 4.5-6.3μm long and 0.9μm diameter, contained within packets 7-30μm diameter and 24-60μm long, lying at a shallow angle to the surface of the epithelium.

Fusiform envelopes measuring 8-18μm long and 2.7- 3.6μm diameter filled with numerous acicular, refractile microrhabdoids 2.7-3.6μm long and 0.25-1.8μm diameter, lie in the epithelium at a shallow angle or parallel to the surface.

Within the dorsal and ventral epidermis are gland cells containing translucent cytoplasmic granules which give a positive alcian blue histochemical reaction for acid mucopolysaccharides. These glands are particularly numerous anteriorly. A distinct cluster of strongly basiphilic glands form a frontal gland complex and open into a antero-ventral pit. Parallel with the dorsal surface is a network of concrement cells which are the iridescent white flecks observed macroscopically.

The mouth opens ventrally and is situated in

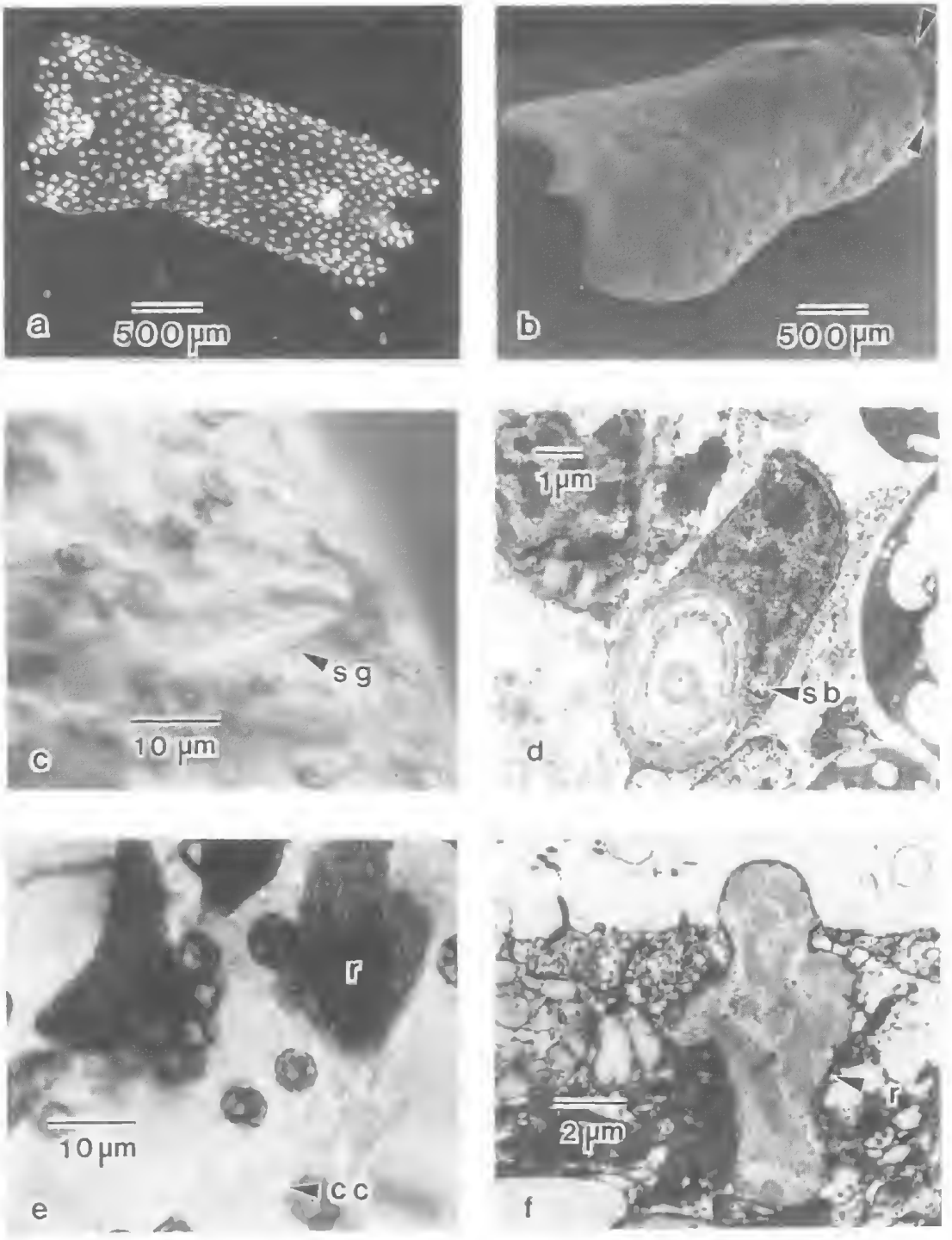

FIG. 3. *Convolutriloba hastifera*. (a) dorsal aspect, living specimen by incident light, and (b) fixed specimen (SEM). Note depressed eye-fields (arrowed) (c-f) epidermal structures: (c) anterior sagittocyst (d) sagittocystoblast (e) pigmented rhabdoids and concrement cell (f) packet of acicular rhabdoids.

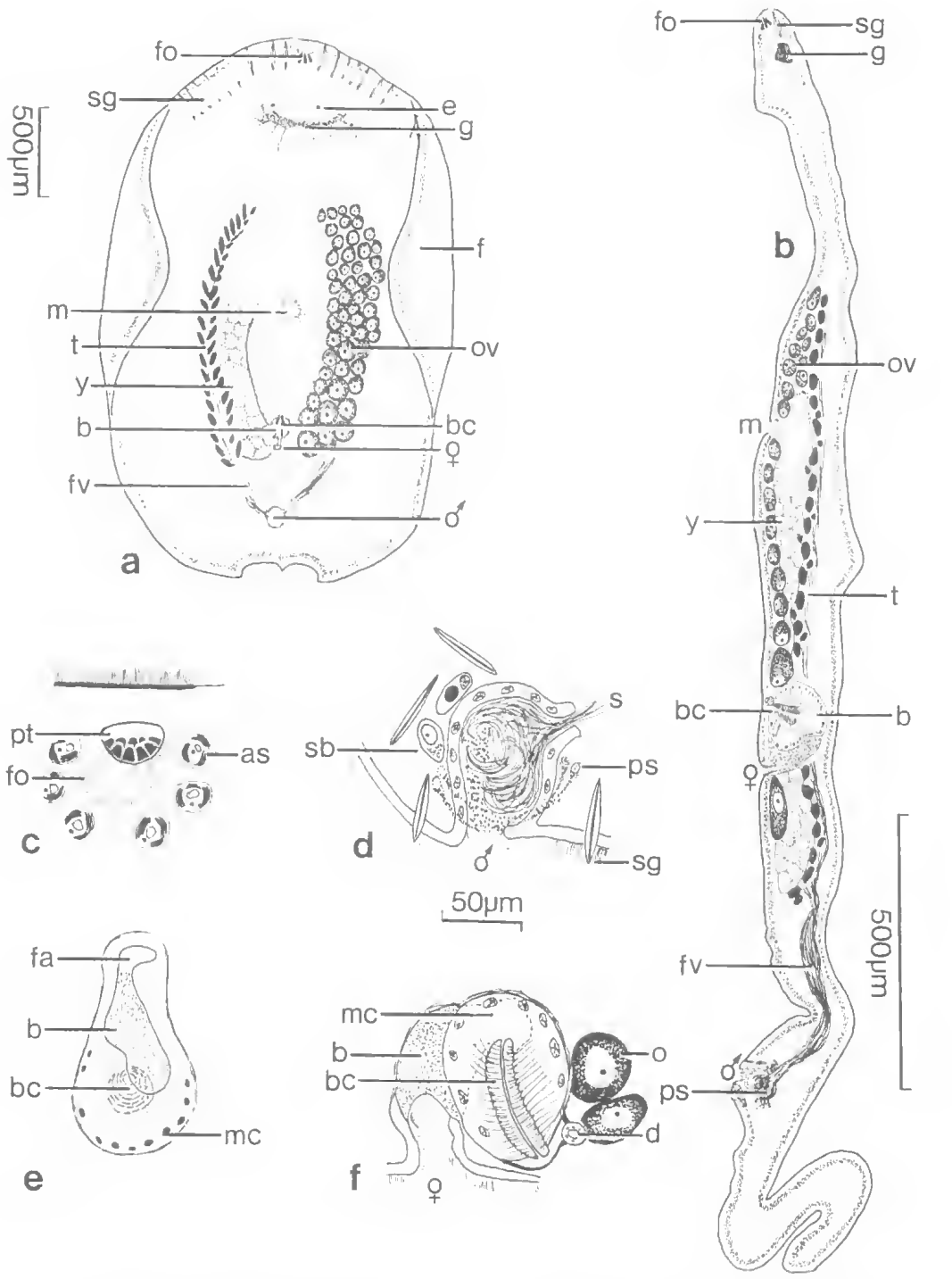

FIG. 4. *Convolutriloba hastifera*. (a) ventral aspect, whole mount (for clarity the ovary is not shown on right side) (b) longitudinal section (c) frontal organ and pit (unscaled sketch) (d) male copulatory apparatus (e) female copulatory apparatus, plan view (unscaled sketch) (f) female copulatory apparatus.

the anterior half of the body. Ingested amphipods were observed in the endocytium of live specimens.

The testes are paired and are distributed dorsolaterally. Sperm pass posteriorly, accumulate in false seminal vesicles then continue into the male copulatory organ. This organ consists of an unciliated chamber filled with sperm. Basiphilic granular secretions form a plug in the genital pore, and are derived from prostatic glands equatorially surrounding the male organ. The male gonopore is ventral and ringed by sagittocysts.

The ovaries are paired and lateral. They are divided into oocyte producing and yolk producing parts. The oocyte-producing portion is ventrad and extends posteriorly 0.5mm from the anterior tip to just behind the female genital pore. The yolk-producing part is dorsad and begins just behind the mouth and terminates posterior to the oocyte portion.

The female genital pore is ventral approximately midway between the male pore and mouth. A short, ciliated female antrum leads into the bursal complex. The bursa is elongate, thin walled and filled with basiphilic granules. It communicates with the proximal end of a single anteriorly-curved sclerotised bursal canal.

SYSTEMATIC DISCUSSION

Hendelberg and Åkesson (1988) noted that the male copulatory organ in *Convolutriloba* is a different type from that of *Convoluta*, but considered the possibility that in their asexually reproducing specimens the male organ was not fully mature. For this reason they expressed some uncertainty as to whether the genus should be assigned to the Convolutidae or Haploposthiidae. The male copulatory organs of *C. retrogemma* and mature *C. hastifera* are similar. This suggests that the male organ described from the former species was mature. Both species lack a penis. *Convolutriloba* is therefore confidently assigned to the Haploposthiidae.

Specimens of *Convolutriloba* from *Tridacna* at the University of New South Wales were nonsexual and unable to be identified fully. The specimens are not *C. hastifera* as anterior sagittocysts are absent. Examples of *C. hastifera* the same size as the Sydney material are found to have anterior sagittocysts. The species is similar to *C. retrogemma*.

Convolutriloba hastifera was first observed in 1976 by Dr John Collins of James Cook University (JCU) on the rocky part of the base of *Goniastrea* sp. and *Platygyra* sp. corals collected from the intertidal zone Geoffrey Bay, Magnetic Island. They were also present in 1976 in the aquarium at JCU, and in March 1981 collected by Dr Clive Wilkinson from the aquarium at AIMS

The characters which clearly distinguish *C. hastifera* from *C. retrogemma* are the presence of batteries of sagittocystoblasts and sagittocysts anteriorly, presence of eyes and an ovary with oocyte-producing and yolk-producing parts. The dorsal pattern of concrement in *C. hastifera* differs from that of *C. retrogemma* (Hendelberg, *in litt.*).

Convoluta japonica Katô, 1951, (and Kawakatsu, 1983) considered by Dörjes (1968) to be a species *incertae sedis*, is now assigned to *Convolutriloba*. *Convolutriloba japonica* (Katô, 1951) comb. nov. is characterised within the genus by the presence of a statocyst, a rounded posterior with disc-shaped terminal adhesive gland, and absence of lateral caudal lappets. Other features accord with the generic diagnosis.

No separate diagnosis was provided by Hendelberg and Åkesson, 1988 for the genus *Convolutriloba*, the generic characters being those of *C. retrogemma*. As other species have now been referred to *Convolutriloba* it is appropriate to revise and emend the generic diagnosis. Unfortunately the presence or absence of caudal lappets is not a reliable generic character in the acoela. Asexual reproduction with reversed polarity has so far only been observed in *C. retrogemma*, and is therefore not included in the generic diagnosis.

In both *C. hastifera* and *C. japonica* the paired ovary is divided into oocyte-producing and yolk-producing parts. At present it is uncertain whether the ovary in *C. retrogemma* is divided into the two parts as in the other species. In *C. retrogemma*, Hendelberg and Åkesson (1988) describe a germ layer in which some cells are considered to be developing oocytes. Other cells present may be yolk-producing. Confirmation of a bipartite ovary in this species must await examination of sexually reproducing specimens.

From the combination of characters which now define *Convolutriloba*, the presence of a paired ovary divided into oocyte-producing and yolk-producing parts distinguishes the genus from all others in the Haploposthiidae. Otherwise this genus is closest to *Pseudohaplogonaria* Dörjes, 1968, which also has a single bursal canal.

Although sagittocysts are present in several

species of acoels they have only received scant attention at the light microscopic level (see Graff, 1905; Ivanov, 1952; and Marcus, 1959). In structure and mode of secretion, but not in size or chemical composition, sagittocysts share many features of a discharge-type rhabdite, defined by Smith, Tyler, Thomas and Rieger (1982). According to these authors the Acoela seem to lack true rhabdites. Further ultrastructural investigations are required to ascertain whether there is any homology between acoel sagittocysts and the true rhabdites of other turbellarian orders.

Convolutidae Graff, 1904
Heterochaerus Haswell, 1905 (emend)

Heterochaerus Haswell, 1905 p.425 ; Bresslau, 1933 p.264.
Amphiscolops Luther, 1912 p.52; Beauchamp, 1961 p.186.

DIAGNOSIS

Convolutidae oblong in shape, with caudal lappets; colouration and pattern due to symbiotic algae and concrement granules; rhabdoids, statocyst and statolith may be present; with eyes; brain insunk; frontal gland absent; mouth ventral in mid-body; ovary and testis paired; male genital pore ventral in posterior third of body; muscular penis surrounded by seminal vesicle; female genital pore anterior to male pore; female antrum ciliated; bursa T-shaped and bilobed, each lobe with two or more tubular bursal canals; in mature specimens a copulatory canal (cf. Laurer's canal) may be present dorsally opening into female antrum.

TYPE SPECIES

Heterochaerus australis Haswell, 1905.

Heterochaerus australis Haswell, 1905
(Fig. 5a-c)

Heterochaerus australis Haswell, 1905 p.425.
Amphiscolops australis (Haswell); Luther, 1912 p.52; Marcus, 1950 p.21, Dörjes and Young, 1973 p.350.
non *Amphiscolops sp.* (*australis* ?) Trench and Winsor, 1987.

MATERIAL EXAMINED

SYNTYPES AM W387 Port Jackson , New South Wales, Australia, found in shallow intertidal rock pools. Approximately 33 Carmine stained serial sections of a group of 17 specimens on a single microslide. The fifteenth section is marked with ink.

VOUCHER SPECIMENS: Collected at Pioneer Bay, Orpheus Island 18° 37'S, 146°30'E, sexual, from sediments, collected J. Gray, 29 May, 1984. G23009 wholemount, picro-carmine. G23010 three microslides of serial horizontal 7µm sections, iron haematoxylin-eosin.

OTHER SPECIMENS EXAMINED: Queensland: Saltwater Creek 19°05'S, 146°28'E, nonsexual, from the surface of stones, subtidal zone in the creek, collected I. Kneipp, 28 May, 1986; Shelly Bay near Cape Pallarenda, Townsville 19°21'S, 146°45'E, non-sexual, from subtidal sediments, collected L. Winsor, 9 August, 1987.

DESCRIPTION

Specimens are spatulate in shape with two elongate latero-caudal appendages, translucent brownish-yellow in colour with a clear margin, 1-2mm by 0.5-0.75mm. The dorsal surface exhibits iridescence under incident light. A statocyst and statolith are present lying midway between two minute eyes. Brain bilobed and insunk. A frontal gland is absent. Algal symbionts, possibly an *Amphidinium* sp., measure 10-14µm in diameter.

Testes and ovary are paired. Female genital pore is ventrally situated 180µm posterior to the mouth and 80µm anterior to the male genital pore. The bursa is bilobed and T-shaped with lobes present as bulbous extremities on the transverse arm. Each lobe contains 2-3 bursal canals. Sperm accumulate in a seminal vesicle which surrounds a conical muscular penis.

SYSTEMATIC DISCUSSION

The copulatory organs and other features of the Queensland specimens agree closely with Haswell's (1905) clear description, and comparison with the syntypes. There are minor differences in length of the caudal appendages of the specimens examined. Those from Orpheus Island have elongate appendages whereas in specimens from Saltwater Creek and Shelly beach the caudal appendages are short and rounded. In some specimens from both sites the caudal appendages are unequal in length, possibly due to accidental amputation of the normally long delicate structures. Variation in the number of bursal canals in each of the two lobes of the bursae of present material is within the range reported for the species. The presence of Laurer's canal could not be confirmed in preparations of the new material.

Heterochaerus australis is characterised by the presence of multiple bursal canals in each lobe of a T-shaped bilobed bursa, rhabdoids, statocyst-statolith, and in mature specimens what may be a copulatory duct between the female antrum and the dorsal surface. The species lacks a frontal organ, and this was the principal reason Haswell (1905) considered *australis* was precluded from the genus *Amphiscolops*, all members of which had this structure. He therefore erected the genus *Heterochaerus* to accommodate this species.

However in a footnote Luther (1912 p53), considering only external features and multiplicity of bursal canals, synonymised *Heterochaerus* within *Amphiscolops*. Luther's action was not disputed in the literature until Bresslau (1933) without comment listed *Heterochaerus* in the Convolutidae, separate from *Amphiscolops*. Reinstatement of the genus was noted by Marcus (1947) who nevertheless included *australis* in a key to the species of *Amphiscolops* (see Marcus 1950) thus tacitly agreeing with Luther (1912).

In his comprehensive treatment of the Acoela Dörjes (1968) apparently overlooked *A. australis* as it was not included in a listing of *Amphiscolops* species. However he obviously accepts the validity of the species as Dörjes and Young (1973) reported the occurrence of *Amphiscolops australis* in Kenya.

To evaluate the systematic position of *A. australis* it is necessary to examine the taxonomic characters of all species in the genus *Amphiscolops* (Table 1). As it presently stands this genus is clearly heterogeneous. Westblad (1946) drew attention to the different types of bursal canals in *Amphiscolops* and with respect to these structures (Westblad. 1946, 1948) remarked on the heterogeneity of the genus. Later Steinbock (1955) commented that the absence of a statocyst in four (now seven) *Amphiscolops* species might possibly justify the erection of a new genus such as 'Alithicum' to accommodate them.

The current diagnosis for *Amphiscolops* is as follows (after Dörjes, 1968):

Coloured through pigment or symbiotic algae; statocyst may be absent; brain insunk; frontal gland weak; mouth ventral; rhabdoids may be absent; posterior as a rule with two pronounced

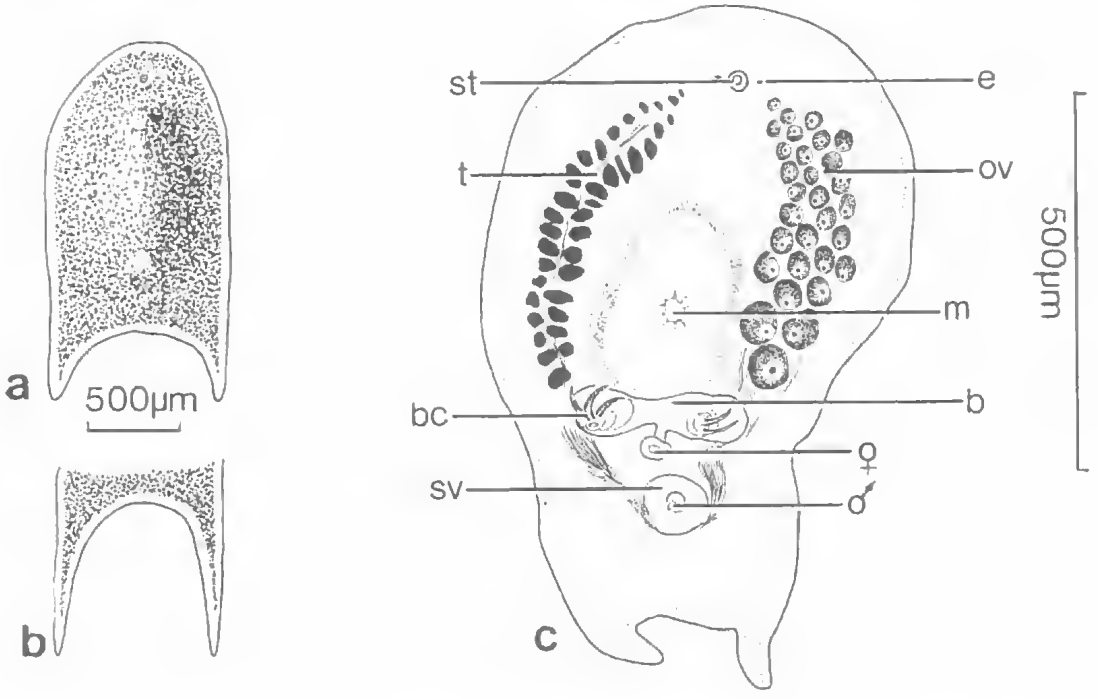

FIG. 5. *Heterochaerus australis*. (a) dorsal aspect, living specimen and (b) with elongate caudal lappets (Orpheus Island specimens) (c) Ventral aspect wholemount (for clarity the ovary is not shown on right side).

SPECIES	AUTHORITY	MORPHOLOGICAL FEATURES																		
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
GROUP 1																				
cinereus$_a$ TYPE	(Graff, 1874);1905	M	5000	R	0	+	+	+	+	+	1	1	BL	L	2		+	T	S	
fulgineus$_b$	Peebles, 1915	M	3000	R	0	+	+	+	+	?	+	1	1	BL	L	2		+	T	S	
reil	Reidl, 1956	?	600	R	0	+	?	+	?	?	?	1	1	SL	C	2		+	?	?	
japonicus$_c$	Katô, 1947	M	6000	F	0	0	+	+	+	?	0	1	1	SP	L	4		+	T	S	
evelinae$_d$	Marcus, 1947	N	2000	F	0	+	+	0	+	0	?									A	
marcusi	Marcus, 1954	J	600	F	0	+	+	+	0	?	0	2	2					V			
GROUP 2																				
bermudensis$_e$	Hyman, 1939	M	2000	T	+	?	+	+	+	+	+	2	1	SL	L	2		+	T?	S	
sp. 2.	Yamasu & Okazuki, 1987	M	1500	F	+	?	?	?	+	?	+	1	1	SL	L	2		?	V	S	
sp. 3.	Yamasu & Okazuki, 1987	M	500	F	+	?	?	+	+	?	+	1	1	SL	L	2		?	V	S	O
GROUP 3																				
langerhansi	(Graff, 1882); Hyman, 1937	M	4600	F	+	0	+	+	+	?	+	1	1	SM	P	6-11 2-8		+	V	S	O
carvalhoi	Marcus, 1952	M	2000	F	+	?	+	+	+	0	+	1	1	SM	P	2-6		+	V	S	V
sp. 4.	Yamasu & Okazuki, 1987	M	2500	F	+	?	?	0	+	?	?	1	1	SM	?	many		?	V	S	O
GROUP 4																				
cf. *langerhansi*	Yamasu & Okazuki, 1987	N	1200	F	+	?	?	0	?	?	+									A	
sp. 1.	Yamasu & Okazuki, 1987	N	1300	F	+	?	?	0	+	+	?									A	
sp. form castellonensis	Steinböck, 1955	N	3000	F	+	?	?	0	+	?	?									A	
sp. form gerundensis	Steinböck, 1955	N	4000	F	+	?	?	0	+	?	?									A	
sp.	Ehlers & Dörjes, 1979	N	2000	F	+	+	+	0	+	0	0									?	
GROUP 5																				
sp. 5.$_f$	Yamasu & Okazuki, 1987	M	5000	T	+	?	?	?	?	?	?	1	1	SM	?	10+		?	T	S	
GROUP 6																				
australis$_g$	(Haswell, 1905)	M	4000	F	+	+	0	+	+	+	+	1	1	TM	L	4-18		+	V	S	O
carpasei$_h$	Hyman, 1939; Marcus, 1950	J	3000	F	+	0	0	0	+	0	+	1	1	TM	L	4-6		+	V	AS	

TABLE 1. Morphological and other taxonomic characters of species of the genus *Amphiscolops*, together with a commentary on species groups within the genus. Group 6 has been transferred to *Heterochaerus* (this paper).

KEY TO MORPHOLOGICAL FEATURES IN TABLE 1.

+ = present, O = absent; ? = not mentioned in original description or uncertain.

1. sexual maturity of specimens upon which description based. N = nonsexual; J = juvenile; M = mature.
2. maximum length reported (in μm).
3. shape of posterior end. R = rounded; F = forked (bilobed); T = trilobed.
4. algal symbiont.
5. pigment.
6. frontal organ.
7. statocyst-statolith.
8. eyes.
9. rhabdoids.
10. concrement cells.
11. number of female genital pores.
12. number of male genital pores.
13. type of seminal bursa. BL = bilobed with paired lateral bursal canals; SL = spheroidal with paired lateral bursal canals; SM = spheroidal with multiple central bursal canals; SP = spheroidal with paired ventral papillae each containing two bursal canals (*japonicus*); TM = T-shaped bursa with multiple lateral bursal canals.
14. type of bursal canal. C = corkscrew shape (*zeii*); L = long tubular; P = papillate, large and small.
15. number of bursal canals; for taxa with bilaterally arranged bursal canals, half this number are present on each side.
16. seminal vesicle + penis sac.
17. posterior position of male genital pore. T = terminal-sub terminal; V = ventral.
18. reproduction apparently by A = architomy or S = sexually.
19. birth of young. O = oviparous; V = viviparous.

NOTES ON SPECIES

a. *cinereus*. Paired vaginae open into female genital duct.
b. *fulgineus*. Eyes with refractile granules. Species may be conspecific with *cinereus*.
c. *japonicus*. Eyes with refractile granules. Adhesive sucker present between mouth and female genital pore.
d. *evelinae*. Antero-dorsal fossa present.
e. *bermudensis*. Frontal organ pit present. Paired vaginae open ventrally.
f. sp. 5. Has two species of algal symbionts (as does sp. 3).
g. *australis*. Dorso-atrial duct (cf. Laurer's canal) present in mature specimens.
h. *sargassi*. Paired efferent female openings where ovarian stroma interrupts ventral epicylium. Seminal bursa in this species and in *australis* differ from the bilobed bursae in other species of *Amphiscolops*.

COMMENTS ON GROUPS

GROUP 1

In all members of the group (which includes the type of the genus), algal symbionts are absent, the male genital pore is terminal in position, bursae have paired lateral tubular bursal canals. The taxonomic position of *evelinae* and *gemitiporus* is uncertain (species *incertae sedis*)

GROUP 2

Similar to Group 1. Algal symbionts present, male genital pore ventral in position, bursae with paired lateral tubular bursal canals. The position of the penis in *bermudensis* is uncertain. *Amphiscolops* would be fairly homogeneous if it was restricted to Groups 1 and 2, with appropriate emendment of the generic diagnosis.

GROUP 3

A homogeneous group characterised by presence of algal symbionts, numerous papillate bursal canals in the bursa, and ventral position of the male genital pore. The structure of the bursal canals apparently differs from those structures in Groups 1 and 2. This group should be separated from *Amphiscolops*.

GROUP 4

All the species in this group have been described from non-sexual specimens. They have been placed in *Amphiscolops* primarily because they have algal symbionts and caudal lappets (bilobed posterior) although the type of the genus lacks both these features. At present these species cannot be reliably assigned even to a family level and are more appropriately regarded as species *incertae sedis*.

GROUP 5

Although little data on this species is available, the large size, presence of two species of algal symbionts, multiple bursal canals and terminal male genital pore suggest it may belong to a new genus reported from the western Pacific (Winsor, pers. obs.).

GROUP 6

This group is characterised by the presence of algal symbionts, ventral male genitalia pore, multiple lateral bursal canals and T-shaped bursae. A frontal organ is absent. This group has been transferred to the reinstated genus *Heterochaerus* (this paper).

posterior lappets; ovaries and testes paired; two genital openings, or they may be manifold, seminal bursa with two or more curved, or corkscrew-shaped sclerotised bursal canals; male copulatory organ complex conical, pyramidal or tubular; a male antrum and seminal vesicle may be absent.

Thorough revision of the genus at present is hampered by inadequate data for many of the taxa. Also some of the characters used to define the genus, in particular the frontal gland and the type, number and position of the bursal canals - key elements in the generic diagnosis - need to be re-evaluated. Ideally this should be undertaken at both light microscopic and ultrastructural levels. However despite these problems species groups within the genus can be recognised (Table 1 - comments on groups) thus indicating directions for further revision.

Of the *Amphiscolops* species for which adequate data are available, those comprising Group 6–*A. australis* and *A. sargassi* Hyman, 1939– are the only members of the genus in which a frontal organ is absent. Both species have similar morphology, in particular the presence of a T-shaped bilobed bursa, each lobe of which contains two or more bursal canals of the same type. As both species exhibit a combination of characters clearly different from *Amphiscolops* Group 1, which includes the type of the genus *A. cinereus*, they should be removed from *Amphiscolops*. Luther's (1912) synonymy of *Heterochaerus* within *Amphiscolops* is rejected.

Heterochaerus Haswell, 1905, is now reinstated and diagnosis emended. Both *A. australis* and *A. sargassi* are transferred to this genus.

Known only from non-sexual (Hyman, 1939) and immature (Marcus, 1950) material *Heterochaerus sargassi* (Hyman, 1939) comb. nov. nevertheless exhibits the essential characters of *Heterochaerus*. Hyman (1939) indicated that in this species there 'are no evident frontal glands nor frontal pit' (her use of the term *frontal glands* referred specifically to the group of glands forming a frontal organ, rather than cutaneous glands which open from the anterior margin). Marcus (1950) corroborated these findings noting 'As glandulas frontais desembocam, por via de regra, separadamente no bordo anterior; excepcionalmente coalescem alguns dutos eferentes delas, simulando um orgao frontal. Fosseta frontal nao ocorre.' Described are cutaneous glands which normally open from the anterior margin; occasionally the ducts of some of these glands coalesce, *simulating* a frontal organ. The statement by Ehlers and Dörjes (1979, p16) that 'Marcus (...) beschreibt zwar ein Frontalorgan für *A. sargassi*..' is therefore incorrect.

The type of bursa, and the type, number and position of bursal canals in *H. sargassi* are similar to those of *H. australis*. In *H. sargassi* the ovarian stroma interrupts the ventral epithelium (Marcus, 1950). These structures may be efferent openings for the discharge of eggs. Haswell (1905) concluded that in *H. australis* eggs were discharged through the female genital pore. However he drew attention to a blind anterior diverticulum in the female antrum which he considered might be a vestige of a temporary passage formed to discharge eggs. Multiplicity of female ducts (vaginae) is known in *Amphiscolops cinereus*, *A. fulgineus*, *A. bermudensis*, *A. gemelliporus* (Table 1) and in *Vulgaru cuspidata*. At present it is not known whether these ducts are copulatory or efferent in function, and whether they are homologous.

The absence of a statocyst-statolith in *H. sargassi* may be a consequence of reproduction by architomy, noted for other acoels (Hendelberg and Åkesson, 1988).

The *Amphiscolops* sp. (*australis* 2) reported from the marine lakes in the Republic of Belau (Trench and Winsor, 1987, p.2) is now considered to belong to a new genus to be described elsewhere (Winsor, pers. obs.). The *Amphiscolops* sp. 5 of Yamasu and Okazaki (1987) may possibly be referable to this genus.

KEY TO FREE-LIVING ACOEL GENERA IN AUSTRALIAN WATERS

The following artificial key is provided to facilitate recognition of free-living acoel genera presently described from Australian waters. It is based upon external features evident in living and fixed specimens. Known distributions and habitats are provided. The key is intended to supplement Cannon's (1986) invaluable guide to turbellarian families and genera. Full identification of acoel taxa requires microscopical and histological examination of sexual living and fixed specimens.

1 Body discoid to obovate in shape, posterior margin rounded or notched medially ..... *Waminoa* (1–5mm diameter, found on hard and soft corals; north Queensland and western Pacific)

1'. Body elongate, posterior pointed or with lateral caudal lappets 2

2. Posterior terminating in single pointed tip, lateral caudal lappets absent ..... *Wulguru* (1-3mm long found intertidally in sand and sediments; north Queensland)

2'. Lateral caudal lappels present, posterior with or without median lobe 3

3. With posterior median lobe ..... *Convolutriloba* (3-6mm long found in marine aquaria Townsville, Sydney and Gothenburg, Sweden; on corals in north Queensland waters; one species without caudal lobes found in Japan)

3'. Posterior median lobe absent ..... *Heterochaerus* (1-4mm long, found in rock pools Port Jackson, New South Wales; in subtidal sand north Queensland; in shallow pools on a sandy beach, Mombasa, Kenya)

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